THE ANCIENT VEGETATION OF OHIO AND ITS ECOLOGICAL CONDITIONS FOR GROWTH.*

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It is generally agreed that the life relations between plants and their habitats are an outcome of certain definite processes linked inseparately with the past. Whatever the possible method of evolutionary advance, whether under pressure of unusual environmental conditions or of different inherent irreversible, limits of organic variability, the behaviour of plants under analytical experimental tests will continue to contribute the generalizations of real interest and importance. The facts and the conditions of the present alone can aid in the interpretation of the past.

The comparatively abundant information which we possess as to the present vegetation in aspect, form, structure and function as related to differences in physical, chemical and biological factors is in striking contrast to the absence of a correlation of similar data as regards environmental conditions during geological periods. From the point of view of Ecology, either as geographic ecology interpreting similarities and differences in vegetation identifiable with factors of latitude and climate, physiographic ecology constituting evidence of more local and genetic forces and concomitant organic response, or physiological ecology which is less floristic in aspect than either of the preceding views and which offers the adequate basis of organic response from experimental evidence of the physiological behaviour of plants under known conditions, to one and all the vegetation conditions of the past are of considerable value, whatever the method of endeavor to understand the factors which the fossil plants record. Those who have confined their ecological study to the environmental investigations of the present must sooner or later test and supplement their investigations by reference to the past. And the aim should be to reproduce not only an accurate fragment of botanical history from the study of fossils and their respective strata, but to correlate structural characteristics with physiological conditions of growth, applying the knowledge of relations gained from living plants. Whether or not the data can be accepted as sound links in the chain of evidence rests largely in the value of the experimental work at hand and in the degree with which they interpret many apparent anomalies.

The limiting climatic and physiographic features which characterize bogs, and the structural features and functions of the vegetation peculiar to them, have seemed to the writer of sufficient interest to invite attention to an inquiry on the probable

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cause of the xerophily of many of the carboniferous plants which lived in swampy areas. The present paper is intended therefore, as a continuation of the ecological studies which appeared from time to time on the vegetation of an Ohio bog and peat deposit. (7–10). The problems involved in the following discussion are by no means to be solved within the limits of this paper; merely an adjustment of perspective is made, leading from a consideration of the fossiliferous plant remains of the coal measures of Ohio.

In attempting to sketch an outline of the geological history of Ohio it is obviously impossible to go into any details of description, or closely follow the development up to the present. At most only the briefest introduction can serve and only a general resume can be noted here. For the specific Geology of the state and a fuller treatment of the subject, the reader is referred to the volumes of the Geological Survey of Ohio and to the literature here cited.

Were we to make a rock section deep enough to reach to the lowest limits of the known stratified deposits, to the great foundations of the continent, the geological strata underlying the state would show as a stage of early growth a predominance of limestone and shale in the lower half of the section, and as a stage of relative maturity widespread horizons of sandstone and conglomerate in the upper half of the section. The strata would characterize the gradual dominance of atmospheric over hydrospheric and volcanic action in a succession of changes, often interrupted and repeated, of which a mountainous elevation and the graded plain near sea level are the extreme forms in the physiographic cycle.

The strata belong to five principal divisions or ages which named in ascending order are as follows: Lower Silurian or Ordovician; Upper Silurian; Devonian; Sub-carboniferous or Mississippian; and Carboniferous, Pennsylvanian, or Coal-Measures. Over the northern and north-western half of the state these are covered by heavy beds of clay, sand, and bowlders which taken together constitute glacial drift. No evidences have been found in Ohio of that group of strata below the Ordovician known as the Cambrian, and pre-Cambrian (Laurentian, Huronian and Keweenawan), or the great series of systems comprising the Mesozoic and Tertiary time divisions. They either left no record within the limits of the state, or much erosion must have taken place immediately succeeding their formation.

Each of the rock systems is again subdivided, and inasmuch as the new stratigraphical divisions are coming into use more generally and are replacing the geological names of the older surveys, the following table taken from Bulletin 7, (21), has been added to show the place in the scale, the relationship of old and new names for the formations, and the thickness assigned to the various formations:

GEOLOGICAL SCALE OF OHIO.

Orton, 1895.	Prosser, 1905.	Thickness
Glacial drift.	Alluvium and Glacial.	0–550′
Upper Barren Coal Measures.	Dunkard formation.	525′±
Upper Productive Coal Measures	Monongahela formation.	200–250′
Lower Barern Coal Measures.	Conemaugh formation.	400–500′
Lower Productive Coal Measures	Allegheny formation.	165–300′
Conglomerate Group.	Pottsville formation.	250′±
Sub-carboniferous limestone.	Maxville limestone.	25′±
Logan Group.	Logan formation. Black Hand formation.	100–150′ 50–500′
Cuyahoga shale.	Cuyahoga formation.	150–500′
Berea Shale.	Sunbury shale.	5–30′
Berea grit.	Berea grit.	5–175′
Bedford shale.	Bedford Shale.	50–150′
Ohio shale. { Cleveland shale. Erie shale. Huron shale.	Ohio shale. { Cleveland shale. Chagrin formation. Huron shale.	300–2600′
Olentangy shale.	Olentangy shale.	20–35′
Upper Helderberg or Corniferous limestone.	Delaware limestone. Columbus limestone.	30–40′ 110′
Lower Helderberg limestone, or Waterlime.	Monroe formation. { Lucas limestone. Sylvania sandstone. Tymochtee member (?)	50–600′
Niagara Group. { Hillsboro sandstone. Guelph or Cedarville limestone. Niagara limestone. Niagara shale.	"Niagara Group." { Hillsboro sandstone. Cedarville limestone. Springfield limestone. West Union limestone. Osgood beds.	150–350′
Clinton limestone.	Clinton limestone. Belfast bed.	10–50′ 50–150′
Medina shale.	Saluda bed.	20′±
Hudson River Group.	Richmond formation. Lorraine formation. Eden shale.	300′± 300′ 250′
Utica shale, not seen in outcrop.		
Trenton limestone.	Trenton limestone.	130′

Thus the LOWER SILURIAN or ORDOVICIAN system includes the lowest of Ohio's stratified and fossiliferous rocks, the Trenton limestone and the several formations of the Hudson River group. They suggest that a broad but shallow arm of an ancient ocean then covered Ohio. (5). As in the following geologic periods, the sediments were derived from the various rocks carbonated, oxidized, and exposed to erosion and solution, the beds of limestone representing for the most part an accumulation of comminuted particles of shells and lime-secreting plants in a clear sea, and the shales representing the deposits of mud made in still water nearer the land. The adjacent lands were probably too low or too far away to yield abundant sand or permit wave-action sufficiently vigorous to keep the mud from settling. Comparatively very few fossil plants of Ohio have been obtained from the geological formations of this period (17); but the records of the life of the era in the United States and in Europe though meager, are sufficient to indicate that development of life was well advanced long before the known strata were deposited, and that less diversity of climate existed than now. The testimony of the ancient organisms implies nearly uniform soil conditions. The plant forms, which in such rocks must necessarily be rare as fossils, were relatively simple, living along the shore and in open water in definite zones, and appear to have varied with the nature and the slope of the bottom, the depth and clearness of water, etc., much as it is today. Immense quantities of microscopic unicellular plants were undoubtedly present as plankton in the protected bays with sandy and muddy bottoms to form the food supply for the large and varied fauna of that time. At the close of that period a folding resulted in an uplift of a broad, flat island-like area about Cincinnati. This arch known as the Cincinnati axis traversed in a northeasterly direction from Tennessee and Kentucky to the lake basin into Canada. From that time on Ohio was nearer sea-level and in places the land areas were so far elevated as to allow sluggish streams and basins, bordered by plants (13, 4, 11).

The UPPER SILURIAN period includes the Saluba and Belfast beds, the highly crystalline Clinton limestone, the several elements of the Niagara group, and the Monroe formation. It extended over a vast period of time, pointing to oscillations of level which covered wide ranges of latitude. The great lagoons and inclosed salt-water basins which were present suffered rapid evaporation. They are signs indicating that an unusually arid atmosphere prevailed. The severity of the conditions restricted life almost wholly to the lowland and the shore of other more favorable regions. Probably the Arctic regions were then the most favorable for growth and development. The fossil plants are few and at times of doubtful affinity; the data are altogether inadequate to give any idea of the vegetation and its ecological conditions for growth. This relative absence of fossils, together with the character of the sediments, the frequent aeolian crossbedding and frequent mudcracks—are the mark of periods of exposure; they point to near-shore deposits if not to land origin, and to conditions of aridity with tropical climate. This does not mean, however, that a prolific vegetation and perhaps of an advanced order did not exist. Though nothing that can be called a land flora existed, or at least is yet known, the plants of the following period show such marked differentiation and the ancestral relations are so uncertain, that a long previous history, or else a rapid evolution and extinction of intermediate forms would be the only alternatives on which to base an interpretation. A number of species common to Kentucky, Michigan and some parts of Europe have been described; among them are Buthrotrephis ramulosa (16), which bears a close resemblance to Galium (Bedstraw), and Trichophycus venosus, regarded as a plant from the Eden and Lorraine formations. The animal fossils have many characteristics in common with the European Siluric.

The sea again invaded the land and submerged it wholly. A general period of quiet prevailed during the larger part of the following, the Devonian Age. Toward the close of the Mid-Devonic renewed emergence was accompanied by erosion. The era includes the Columbus and Delaware limestones, and the Olentangy and Ohio shales. Where the changes in the relations of land and water were favorable, a rapid intercontinental migration and expansion of life followed, checked only by barriers and by occasional submergence. The record of plants (18) is too imperfect in Ohio for definite discussion, but fossil evidences show that gigantic marine algae were abundant in the seas together with fish and ostracoderms, while on the land-islands then exposed, there were insects, and mollusks, and in the flat lowland surfaces were broad marshes covered with plants, the larger number of which were herbaceous and highly differentiated. The Devonian plants of contiguous areas show no annual rings to bear evidence of seasonal changes in temperature or intervals of prolonged drought (25). The flora is far richer than that of the Silurian, and of great botanical interest, since in this period occurred great migrations of plants from the Arctic regions, and the development if not the actual beginning of land plants. These facts suggest distinct edaphic as well as other environmental changes. The great inland basins contained a vegetation archaic in many features yet not unlike that now living in swamps and in the tropics. The plants were largely the primitive forerunners of ferns and their allies, and the lower fern-like gymnosperms with an undergrowth of soft thallose forms, very much like the liverworts of today; their decay was accelerated by bacterial action (22). The Devonian types were in many respects similar to those of the Carboniferous period, and as the latter are much better preserved and represented in the Coal flora, a conception of their ecological conditions for growth may be deferred with advantage until the discussion of that period.

A renewed expansion of the sea entrapped the fauna and flora in beds of sediment of great depth. This organic matter is the chief source of the oil and gas in use today. It is impossible as yet to state with certainty how these fuels have been formed and concentrated. Chemists suggest an inorganic origin for these products. It is thought, and the theory is supported by laboratory experiments, that the great supplies of petroleum were produced through the agency of iron carbides within the earth, generating the hydrocarbons upon access with percolating water. But the quantities traceable to such a source are insignificant in comparison with the great repositories containing the oil. Buried accumulations either of plants, animals or both can alone account for the origin of gas and oil under the observed conditions. The production of hydrocarbon compounds has been studied in coal mines as the "fire damp," in bogs and swamps as "marsh gas" and in the fermentation of cellulose by anaerobic bacteria. Seaweeds and diatoms are known to contain globules of oil; other oily substances of organic origin are the "cholesterol" found in plants and the fatty parts of animals. The optical phenomena of organic oil, that is, the power of rotating the plane of polarization of light, is not shown by inorganically formed hydrocarbons. In nature an accumulation of organic debris, the exclusion of air, and the existence of an impervious protecting sedimentary stratum seem to be the essential condition toward rendering the process of distillation and transformation possible. It is often surprising the quantity of oil which an apparently dense rock stratum can hold. Pressure, temperature, viscosity, the nature of surrounding rocks, and a flow of the liquids and gases into porous rocks and cavities, no doubt, must all be taken into account when considering the changes involved in the origin of gas and oil; but at present the organic origin of these fuels seems to have the strongest support (2).

The SUB-CARBONIFEROUS or MISSISSIPPIAN period which followed the interval of widespread submergence consists of the Bedford shale, Berea grit, the Cuyahoga, Black Hand, and Logan formations, and the Maxville limestone. An increased land area gave increased contact between the atmosphere and the rocks. In the western half of Ohio the period was one largely of sea extension. Disintegration and much erosion must have taken place to give the sedimentary material of the equivalent formations. A gulf which extended east of the great arch-island enabled plants as well as animals to flourish in isolation for a period sufficiently long to differentiate species of its own. For Ohio the record of plant life is poor (24). But enough fossil vegetation has been recovered in the surrounding states to show that all the leading groups of the Devonian flora were represented with an associated insect life. The different areas exhibit distinct floral and growth-form differences, and suggest either barriers or differences of water content in the soil. The plant associations are varied and of several aspects. The vegetation is remarkably cosmopolitan in distribution which would premise the absence of climatic zones. Many plants exhibit a striking xerophily; the leaves are reduced to linear organs, the stomata have special constructions and are heavily coated and hardened; the stems show development of water storage tissue; the roots are extended horizontally. The general desiccation effects of the habitat resulted, however, not in the extermination of plants favoring free water, but in the limitation of their functional activity to periods of moist or rainy seasons and in the increase of functional responses. The differentiation has become a factor in distribution and has given the plants a greater range of dispersal; the new place-functions had a survival value in the competitive struggle among the organisms, and in the environmental selection. These phenomena, as will be shown below, are not suggestive of greater severity of climate, but indicate unfavorable conditions in the peaty substratum of the marshes.

The era was brought to a close by an emergence of considerable areas of shallow lowland which with their vegetation constitute the great CARBONIFEROUS or PENNSYLVANIAN system and its important Coal-measures. The land area of Ohio grew in spite of the fact that it was periodically depressed and degraded. The withdrawal of the sea ultimately resulted in the union of separate land masses and the extension to its present borders. The formations are a series of beds somewhat unlike any heretofore considered. Irregularly distributed through the Carboniferous series are six or eight strata of sandstone, part of them conglomerates, characterized by the presence of quartz pebbles which sometimes are of large size. Next to them are beds of shale in great variety of colors; they are frequently replaced with sandstone layers or sheets of limestone. The former are frequently crossbedded, the agents of deposition being rivers or the wind; the latter are all of them thin and partly of fresh water origin, and partly of marine origin as is shown by the abundant fossils which they contain. The limestones are in many cases deposits of a calcareous nature, and frequently associated with beds of iron ore or with a layer of clay of varying degree of purity. The clays are always overlain with seams of coal ranging from a mere black line to a dozen feet and more in thickness. Each of these coal seams stands for a former low and undrained land surface and its vegetation cover. The well-marked order of arrangement of the strata underlying the coal seams is intimately connected with a long-continued growth, sudden submergence, and subsequent fossilization of marshes adjacent to an ancient sea, and of great inland xerophytic vegetation formed in island-like masses very much like the peat bogs of today, but over much wider areas than any single present day bog occupies. The Carboniferous system includes the Pottsville, Allegheny, Conemaugh, Monangahela and Dunkard formations, all of which have been described in great detail in the later volumes of the Geological Survey. Over these rocks of at least two-thirds of Ohio are spread in varying thickness the deposits of the glacial drift. The glacial formations of Ohio have been very fully described by Leverett (12); a brief account follows in another paper in connection with the present distribution of vegetation in Ohio lakes and peat deposits and the physiography of the state.

The mode of arrangement of all geological formations is that of sheets resting one upon another, but not horizontally. Slow and comparatively gentle movements of the earth's crust, unaccompanied by fractures or displacements have given rise in the state to a system of northeast and southwest foldings. The most important of these is, as has been stated at the outset, the Cincinnati axis which traverses the state as an arch from Cincinnati to the lake shore and beyond into Canada. The other lines of elevation are relatively weak and come into Ohio from Pennsylvania and West Virginia, and are known respectively as the Appalachian fold, the Fredericktown and Salisbury anticlines, and the Wellsburg, Cadiz, and Cambridge anticlines, located near places of that name. They are undoubtedly folds of the great series to which the Allegheny mountains of Pennsylvania and West Virginia belong. This emergence of the rocks of the state has its approximate date at the close of the Lower Silurian period, and has never been more than a low mountain chain.

Along a large part of the Cincinnati axis the strata which once arched over it have been extensively worn away. They are found resting in regular order on either side. The geological map of Ohio recently published shows the areas covered by the principal systems and their series of strata. In the region about Cincinnati the erosion has been greatest, exposing there the oldest rocks. The direction of the draining streams of the western half of the state has been mainly determined by this great anticlinal axis. It forms the divide between the waters of the Scioto and the Miami, and between the Sandusky and the Maumee. On the east side of the anticlinal axis the rocks dip down into a basin in which all the strata form trough-like layers, their edges outcropping eastward on the flanks of the Allegheny mountains. The older rocks are deeply buried, and the surface is here underlaid by the highest and most recent of rock formations, the Coal-measures or ancient vegetation deposits. In the northwestern corner of the state the strata dip northwest from the anticlinal axis and pass under the Michigan coal basin, precisely as the same series east of the anticlinal dip beneath the Allegheny coal field, of which Ohio's coal area forms a part.

The well-marked order of arrangement which the coal fields of Ohio present, suggests that at the beginning of the Carboniferous age an arm of an ancient shallow lake extended inland and continued in an unbroken sheet up to the Cincinnati arch which made its western boundary. Year after year for many centuries an exceedingly dense luxuriant growth of vegetation covered the surface of the shallow basins as scattered swamps and bog-like marshes sometimes running into a long connected chain, and sometimes quite isolated. The vegetation was doubtless of many kinds of trees, especially giant ferns and club-mosses, with an undergrowth of shrubs, and plants like grasses and sedges. There were many minor differences between the vegetation of different basins; zones of predominating lycopods alternated with ferns. The vegetation must have moved into the open water of protected bays and inland water basins progressively, as groups, distinct in physiognomy and growth-form, the zones varying in width with the definite conditions of life and the selective action of the habitat. The plankton formation must have been followed by plants nearer the margin and submerged along the gently sloping shore lines. Free floating forms similar to Azolla, Salvinia, and to various algae must have existed in great masses, easily transported by winds and currents, at times completely covering the quiet pools. As their debris formed a slowly rising deposit in the basin, the littoral or shore formation must have advanced toward the center of the water basin forming a mat of interwoven rhizomes and roots, harboring various societies and layers according to the light and water conditions. In time the basin became filled with the debris of the vegetation. In many cases the vegetation accumulated to a depth of more than fifty feet, but this great distance from the mineral substratum or the deficiency of mineral substances never rendered it difficult or impossible for the plants to grow luxuriantly. Green plants utilize water and the carbon dioxide of the air to form food, the starches, sugar fats, and proteins necessary to their nourishment and for the successive phases of a normal development. The mineral soil-constituents are not the food of plants; they are indispensable but their amount is very small in organic substances, and alone they are incapable of sustaining life in plants.

Trees standing erect within a bed of coal, their horizontal roots still embedded in the underlying stratum; the corky bark, the wood, branches, leaves, spores, and fruits of many plants, and even the remains of fosil micro-organisms (22) have given their testimony to what once existed. Though not reported in the Coal-measures of Ohio, the aggregations and often large masses of resinous bodies, amber, fossil coral, and a multitude of similar substances by their varying quantities show the exact character of the vegetation. With the flora many animals commingled; and where they were most abundant, their fossil remains are found. Little is known of the characteristic plants of the upland vegetation. There are descriptions of about 150 species for Ohio (14, 19, 24, 25), but most of the interesting fossil plants were found in the roof of Coal No. 1, that is in the marshes near the base of the Coal-measures. In Ohio this stratigraphical position is "more than two thousand feet above the base of the series, as revealed in the geosynclinal basin of West Virginia, which was first filled with strata of the Coal-measures and long before any similar formations took place upon the ancient marginal Waverly plateau of Ohio" (1.)

The flowering plants (Anthophyta) had not yet appeared. Bacteria (22, 23) and other fungi were present, no doubt, in great abundance. Liverworts and Mosses (Bryophyta) were probably in existence but they still held an unimportant place. There were principally ferns (Pteridophyta) which at this time had reached their greatest development and differentiation. Their first appearance is as strange and distinctive among plants as that of the brachiopods among the animals. They were in part more primitive than now and in part more advanced representing transitional types; but they surpassed all other forms in number and persistency of type. There were scouring rushes (Calamophyta) of much higher and varied organization and of greater height and diameter than the present forms. The several species of the Sphenophyllales long since extinct, were of tree-like aspect, bearing small wedge-shaped leaves, and sporophylls in cones; most of them are found as undergrowth beneath the shade of giant lycopods. The Equisetales had hollow jointed stems with very small narrow leaves; they are mostly extinct plants of which but one genus, Equisetum, has survived. The Calamariales also long since extinct, grew in dense thickets; they often were of tree-like aspect and dimensions, with narrow distinct leaves in which the stomata were deeply set. The branches and leaves were placed in whorles on jointed hollow stems which arose from underground rhizoms and increased in diameter by the growth of a cambial zone; their wounds were healed by a development of cork. There were the Lycopods (Lepidophyta) the largest of the carboniferous plants, in the form of Lepidodendron and Sigillaria, both with long needle-shaped leaves and stomata in deep furrows on the under side, often protected by a hairy covering; the trees were surface-rooted, the roots spreading out in all directions from the trunk. There were the Cycads (Cycadophyta), fern-like gymnosperms related to the modern conifers and flowering plants of which indeed they may have been the ancestors. Of these the best known are Cordaites, Megalopteris, Alethopteris and possibly Lyginopteris with its spiny stem and highly dissected xerophilous foliage, Bennettites, and perhaps Ginkgo. All these were strikingly cosmopolitan in distribution, extending to high latitudes. They were at their climax of vigor and height, and verged into more recent types.

How the coal fields were formed hundreds of centuries ago may be seen at any of our lakes today. Our lakes and ponds represent only one of the several conditions under which vegetable matter accumulates. Other but less important ways possible to form coal beds are accumulations (1) built up from the ground by successive elevations of the water table; (2) in sea bottoms beneath "sargasso" vegetation; and (3) in marine swamps including mangrove swamps and coastal salt marshes. The slight admixture of sediment which indicates the absence of waves, tidal currents, wind-formed currents and eroding rivers, and the fact that at present only one kind of tree, the mangrove, grows in salt-water, is against the view that the coal was formed in salt-water. No records exist to show that in earlier ages the vegetation of the ocean differed greatly in kind from that now predominating. Ferns and mosses are entirely absent from the ocean; the main marine vegetation is still formed by algae, often highly differentiated, which belong to diverse orders. The manner in which the bed of vegetable matter accumulated, and how it was kept from decay, is a long and interesting chapter. The process has been described elsewhere (10) in more detail.

Critical periods suddenly arrived, possibly subsidence accompanied with a deluge of water from an adjacent sea, lake or aggrading stream, carrying silt, burying the vegetation under deposits of mud and sand and converting the submerged portion into dry land. The rise in water level brought with it the recurrence of swamp conditions, but the succeeding shallow lake had a narrower area than its predecessor, and around its shores and in island-like masses flourished again a dense luxuriant vegetation. In long-continued growth it existed, filling the lake with an accumulation of vegetable debris to the depth and the margin which it still retains as the present coal field. During its formation the nature of the sub-soil on which the vegetation grew, and the drainage relations affected then as now the character of the plants predominating in an area, and thus influenced the percentage and kind of ash in the vegetable debris. Frequent local or general disturbances in topography and sedimentation during times of flood brought about the occurrence of partings and seams in coal beds. Not infrequently the vegetation was buried under sheets of limestone that accumulated through precipitation in the invading water. In the subsequent submergence and fossilization there followed other marshes and bog-like swamps. These coal beds represent in some places submerged forests, and in others the coal was probably formed not by the slow growth of vegetation in situ, but from drifted vegetable material. But every successive coal forming area had a narrower lowland basin than its predecessor. This indicates that the changes in the relative level of water were not accompanied by oscillations in land level.

The geological evidences of the earlier periods of the state's development show that CO_2 existed in much larger quantities than now, since enormous amounts have been fixed in the beds of limestone. The depletion of the CO_2 content, it may be presumed, produced effects on the atmospheric blanket which tended to lower the average temperature and moisture and this changed the climatic character of the region (5). Similarly the tremendous amounts of carbon stored in the basins of the coal measures by the work of green plants undoubtedly produced a marked effect on the atmospheric content of carbon dioxide. Far reaching changes in climate must have followed, such as are exemplified in the periodic glaciations of the Pleistocene.

The duration of the Carboniferous period must have been a very long one to yield deposits of coal of such thickness, for it should be remembered that a large part of the vegetable matter, about four-fifths, escaped as gas in the making of coal, and the remainder has been compressed to a fraction of the original layer of vegetable debris. It is estimated that from 15 to 30 feet of peat are required to make one foot of coal. By a series of changes which are plainly traceable, vegetable matter, peat, lignite, bituminous or soft coal, and anthracite form a series of substances which grade one into another in an unbroken line from complex organic partly oxidized compounds at one end to nearly pure carbon at the other. The succession is not necessarily a strictly lineal one, since degree of decomposition and chemical changes, previous exposure of the vegetation to reduction action or to oxidation, affect the alterations in various ways. The metamorphic changes are hastened where the structural condition of the overlying rock favors the escape of the gaseous products. Ligno-cellulose compounds are the initial substances which gradually loose carbon dioxide, marsh gas and water, and so yield the series of products represented by the different kinds of coal. Chemical analysis (3) in which the probable combination of elements is given grouped as moisture, volatile hydrocarbons, fixed carbon, ash and sulphur show that the value of coal for fuel is determined mainly by the relative amounts of its volatile hydrocarbons and the fixed carbons. The former represents the free burning constituents of coal and the latter its heating power. Ash and sulphur illustrate the objectionable impurities. Up to a certain point the fuel value or fuel ratio of coal can therefore be determined by dividing the fixed carbon percentage by that of the volatile hydrocarbons. A number of different kinds of coal are recognized in the United States whose differentiation depends largely upon these characteristics. But in whatever variety of form, coal is derived from vegetation which grew in lowland, in ponds and lakes in a manner as we find in sub-tropical swamps and in peat bogs of temperate and northern regions today; it was buried under successive layers of matter like itself, and of sediments such as sand and clay; thus protected from atmospheric oxidation and subjected to gradually increasing heat, and the pressure of overlying porous rocks, the vegetation became transformed to the form we now use. The search for coal today is a search for these ancient marshes, bogs and swamp-forests hidden under layers of sandstone, shales, and drift (20).

What Conditions Determined Xeromorphy and the Origin of Land Plants.

The characteristic xerophily of the carboniferous vegetation has been interpreted by geologists (5) as indicative of a warmer, moister atmosphere, more heavily charged with carbon dioxide than at present. To the writer the facts are hardly consistent with the external conditions assumed. The supposition that xeromorphy involves factors of climate is not necessarily wrong, but calls for a fuller consideration and comparison along with additional factors, the character and magnitude of which is capable of producing like results. A more satisfactory interpretation of the phenomenon of xerophily would be found in the fact that the present vegetation of undrained swamps and of bogs has many of these xerophytic features none of which are correlated with atmospheric influences only. The chief cause for both the xerophily of the coal flora and the great accumulation of vegetable matter is not to be looked for merely in climatic implications. High temperature and humid air promote in a high degree decomposition. The great thickness of the deposits suggests rather that the preservation of the debris was favored by a temperate climate and by agents in the soil such as are involved in the accumulation of peat today. Similarly the force of the inference from the xerophytic aspect of the carboniferous vegetation—namely, the peculiarities of leaf size and leaf structure for maintaining a balance between supply and loss of water—gives additional support to the view that the plants encountered adversities of soil-water content rather than of climate. A satisfactory explanation of the phenomenon has been found in the experimental investigations of the writer on the reduction action and toxic character of bog water and bog soil (10), the results of which are briefly as follows: Poorly drained and undrained water basins and lowlands whether in areas characterized by limestone formations, by sandstone, or glacial drift, become physiologically arid habitats with the accumulation of vegetable debris. Although water is so abundant in bogs and swamps, yet it is largely unavailable to the plants on account of various decomposition products due to the activity of low organisms in the debris-substratum, especially such saprophytes as bacteria and fungi. Peat soils contain bacteria and other fungi in greater number than supposed hitherto, inducing diastatic, inverting, proteolytic, cytohydrolytic and reducing action in the upper layer of the substratum. They vary in kind and number with the nature of the substratum, and show marked interdependence as well as antagonistic action. It has been found that as a general rule there is an accumulation of injurious substances which must be removed if no deleterious action is to follow, and if complete decomposition of the debris is not to be retarded.

The complex and rather ill-defined "humus acids," more specifically humic, ulmic, crenic, and apocrenic acids, are not the important constituents to which peat owes its antiseptic properties and which interfere with the action of bacterial organisms. In Ohio peat deposits, at least, the presence of injurious substances in the substratum is not in direct relation to acidity in the soil. Tests on the reducing powers of peat soils show that the wind driven aeration has little effect on the peat substratum beneath the two-feet level. A shallow superficial zone of oxidation exists in peat soils, and the debris below this is sometimes so charged with injurious decomposition products and gases, and so far unaerated as to be inhospitable to all organisms but anaerobic bacteria.

In the growing season the temperature of peat soil in the more xerophytic of the succeeding bog associations is not below that of other soils. Rapid and passing changes of air temperatures and the occasional extremes do not affect the substratum temperatures. Only average effects prevail and the great periodic changes of the dominant climate. The temperatures of the deeper peat strata indicate that there is scarcely anything of a seasonal descent analogous to the circulation or "overturn" in lakes or in ocean.

The continued growth and persistence of the closely related plant association and the slow succession of vegetation types in a habitat of that character is no longer incomprehensible if we remember that the vegetation grows on top of the accumulating debris and that the water table is always at a high level. The disturbance of the balance produced in the soil is thus not unfavorable to the dominance of the associations. There occur natural successions which are determined, however, not by a deficiency of mineral nutrients, but by an excessive, defective or preventive action in the substratum. The lack of mineral constituents such as lime, potash, and phosphoric acid does not even render it difficult for mesophytic shrubs and trees to invade and grow as the deposit is built up and oxidation processes become prominent in the surface layer of the substratum. To what extent bog plants require the organic compounds arising in peat soils is still undetermined. The assimilation of organic nitrogenous substances is undoubtedly made less difficult on account of the number of saprophytic fungi and the endotrophic mycorhiza usually present.

The characteristic foliage of bog plants is distinctly an effect to a habitat with a moderate or scanty physiological soil-water content. Extreme xeromorphy is reached in the upper layer of open shrub associations; here the CO_2 percentage of the vertical gradient is least and approximates that of the free air; the combined effect of the intensity of light and the greater saturation deficiency of the air is provided for by an increased thickness of the mesophyll layer in the foliage to minimize disturbances in the carbon dioxide supply. This and the narrow leaves with restricted stomata confined to deep furrows and in some cases protected by hairs, wax, or heavy cuticle, are devices common to plants in bogs where the plants must protect themselves against unfavorable water content in the substratum, and not against unfavorable atmospheric influences. The aerial parts of plants are constantly losing water by transpiration, a process similar to evaporation but controlled by the plants within certain limits. To re-establish equilibrium this water loss is replaced by the supply of water from the substratum by root absorption. The taller plants are thus subjected to a difficulty in maintaining the balance between absorption and transpiration in the same manner as are plants living in deserts or in sandy regions. Though the amount of transpiration exhibited by plants is partly influenced by the physical conditions of the atmosphere such as temperature, humidity and wind, yet these factors are much more uniform than are the amounts of available water supply. The limitations of this paper do not permit going into greater detail in respect to the nature and the degree of toxicity in bogs, or in respect to the kinds of plants or the parts of plants which are most affected.

The nearest analogue of the accumulation and the conditions of growth for the vegetation of the coal measures are the bogs and marshes of today. Were there no other trustworthy records of the occurrence of bacteria and fungi in Palaeozic times (22), it would still be a natural supposition that these organisms were abundantly represented, and produced physical and chemical changes in the substratum. The transformation products of whatever nature checked the activity of the roots of plants and depressed their transpiration. The striking similarity of the aerial shoots of the carboniferous plants to those of modern times in bogs and undrained swamps restrain one, therefore, from assuming that the atmosphere differed greatly in temperature and humidity, or was different in the chemical constituents from what it is now. There may have been moderate variations in the carbon dioxide content of the air, but this would require experimental proof upon bog plants and the groups of plants similar to those which lived in carboniferous times, the scouring rushes, the lycopods, ferns, cycads and gymnosperms, to assign its limits. The statements in current literature as to the strengths of that gas which green plants can endure are conflicting (6), and call for further work in the field and in the laboratory.

The consideration of these facts leads to another point—the inevitable conclusion that the form characters and the fundamental resistance to drought and dessication distinctive of xerophytic plants whether in bogs or deserts must have made their appearance within early geologic time. They are not of recent development (15). The climate of northern America has undergone oscillations between periods of maximum aridity and maximum precipitation and humidity, with extreme variations in temperature during and following the several glacial periods; the amplitude occupying periods of perhaps many thousands of years. Variations in climate so wide apart indicate an almost complete change in the character of the flora during the geologic periods. The xerophytic features which characterize bogs and deserts are not to be taken, therefore, as having come about by a direct and continuously increasing edaphic or climatic aridity. Aside from the question as to the methods and the activating conditions in evolutionary development, it seems certain that the origin of xerophytic forms is not one of recent development in the vegetable kingdom but must have been concomitant with the diastrophic and gradation processes of the great geologic periods. The great floral evolutions of geologic history were principally one of growth-form, physiognomy, and functional behaviour, and not of floral structure alone. Water has always been the most important of all the life relations in the environment of plants. In the early types of gametophytic vegetation it remained necessarily of greatest importance for the movements of gametes in effecting fertilization and for dissemination. The luxurious development of these forms in the ancient areas of low lying land became checked in the stress of aridity encountered with the accumulation of their debris. With the origin and the development of the sporophytic types of vegetation, which were from the first less dependent upon free water, the prolongation of vegetation activity enabled the plants to occupy the areas with greater habit reactions. The effects of dessication in the physiologically arid habitats resulted in greater differentiation of organs, in protective and resistance features (9), and in a greater range of dispersal. The vegetation had now developed to forms capable of occupying dry land, and able to maintain themselves as bog or desert vegetation in localities restricting functional activity. The general movement finally resulted in a land flora of which the mesophytes are the highest expression. The lowland basins and regions of coal formation were undoubtedly the regions of the evolution of the flora as a whole and of the several natural plant formations which include many diverse species in a unity of characteristic physiognomy and growth form. Probably the arctic regions were then the most favorable for the growth and development of xeromorphic forms. Migration from northern centers of dispersal, the periods of climatic aridity, and the changes immediately before and after ice invasion, undoubtedly accentuated the ecological evolution of this type of vegetation.

The extensive change in floral types which is particularly evident through the subordination of the ferns to grasses and heath plants, and the elimination and replacement of the primitive gymnosperms by the later gymnosperms and angiosperms is largely one of range and variability of protoplasmic forces. In some types the characteristics often bear no apparent relation to the environment and are retained under the most varied conditions, yet many other types are profoundly and rapidly modified by changes in climate, physiography, and soil processes.

The great development of form in response to the environmental stress was attended by a rapid and luxuriant expansion in range, in successions of vegetation formations, and in sequence of associations. Several forms of cycads, Bennettites and conifers now inhabit desert areas. Not less interesting is the fact that many species of heather-plants of Europe such as Calluna, Empetrum, several species of pines (Pinus sylvestris, P. montana), Juniper (Juniperus communis), birches (Betula, pubescens, B. nana), Labrador tea (Ledum palustre), bladderwort (Utricularia cornuta), and others, can grow both on extremely dry, warm soil and on extremely cold or wet soils. The observation has repeatedly been made by the writer that in the northern parts of Michigan several species of bog plants leave the peat soils entirely and are only found upon dry and poor soils. This is notably the case with tamarack (Larix laricina), the chokeberries (Aronia nigra, A. arbutifolia), the blueberries (Vaccinium corymbosum, V. canadense), the black huckleberry (Gaylussaccia bacata), the shrubby cinquefoil (Potentilla fruticosa), sweet gale (Myrica gale), the steeple bush (Spiraea tomentosa) and several other xerophytes of the peat bogs of Ohio. The cranberries (Vaccinium sp.), creeping snowberry (Chiogenes hispidula), and wild rosemary (Andromeda polifolia) occur in moist ravines and rich woods, while leather leaf (Chamaedaphne calyculata), the buck bean (Menyanthes trifoliata) and Labrador tea (Ledum groenlandicum) are found along slow streams. The majority of these plants occur in Europe and Asia, in habitats of similar conditions. They are bog plants only in the southern part of their range. This departure is in no sense an adaptation to climatic influences but is an equilibrium relation or balance between the absorbing organs, the conducting shoots and the transpiration surface against drought conditions common to either habitat. The structures and distribution habits are induced by physiological aridity or poverty of available water; morphological limitations in the conduction of water do not play a role. The physiological water relation alone must be taken into account for the form and habits of bog and swamp xerophytes, even if the plants inhabit regions of pronounced rainfall and milder temperatures. The appearance of such differentiation can not be taken as one of rapid and notable evolutionary development or as one of the most important in the history of plants; nor would it be safe to assume that bog and desert floras owe their origin to gradual adaptations resulting from the action of climatic changes. The possibilities of survival are very great for forms thrown into the complex conditions of a locality where the functional and structural capacities are suitable for the limiting physico-chemical factors encountered in the habitat. The plants are functionally fitted to occupy the place in a zone with its system of factors. The qualities of growth which enable competition and the crowding out of other forms are not of primary importance in the struggle and selection where physiological capacities have the survival value for activity during drier seasons. Invaders would not exclude the forms by which a bog or a desert is characterized, except where the influence of external conditions has produced irreversible changes in a hereditary line. The structural alterations in roots and shoots of bog plants can not be looked upon as of comparatively recent origin. The phenonemon of xeromorphy has exhibited itself too generally in a variety of plants of conditions in space and time; as such it is the general response in plants to minimize or balance disturbed physiological water relations.

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